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Influence of Water Abstration on Invertebrates in Three Mountain Streams that Varied from Mild to Severe Flow Alteration

Influence of Water Abstration on Invertebrates in Three Mountain Streams that Varied from Mild to Severe Flow Alteration

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Abstract

Invertebrates were compared upstream versus downstream from diversions on three small, headwater streams in the central Rocky Mountains. These streams varied from mild (some aspect of all natural flow components was transfered downstream) to severe (nearly 100% of the flow was diverted for 10 - 11 months of the year) flow alteration. The analysis was separated into seasons of frequent (the diversion gates were often opened and closed; April to October) and infrequent (stable low flows due to constant diversion; November - March) flow fluctutations. Invertebrates appeared resilient to mild flow alterations as neither the abundance, diversity, nor spatial and temporal variation in abundance and diversity differed upstream versus downstream during seasons of frequent or infrequent flow fluctuations. However, downstream total invertebrate density and diversity (especially mayflies) was lower in a severly diverted stream during the season of low flows and infrequent flow fluctuations. Downstream invertebrate density declined by 57% while 10 relatively abundant taxa upstream were absent downstream. If not for an increase in taxa capable of exploiting low flow conditions (chironomids, Ameletus spp., and ostracods), downstream invertebrate densities would have been vastly reduced. Although all taxa in the severely diverted streams recovered (drift) during frequent flow fluctuations (spring and summer), spatial and temporal variation, as indicated by differences in the coefficient of variation, in both density and the occurence of invertebrates (number of taxa) was significantly greater downstream. Depending on the frequency with which free-flowing conditions are re-established, many invertebrate populations (especially mayflies and some stoneflies) will decline and even go temporarily extinct (e.g. Hesperoperla pacifica, Megarcys signata, Neothremma alicia, Polycelis coronata). Downstream communities in the

heavily diverted tributaries appeared to fluctuate between two stable endpoints; a low-flow community dominated by chironomids and ostracods and a more abundant and diverse natural-flow community dominated by mayflies, chironomids, stoneflies, and ostracods.

Introduction

Snow-melt run-off provides water for human consumption in the central region of the Rocky Mountains. Most watersheds in this region contain several small diversions which capture surface run-off at higher elevations and transports it to reservoirs at lower elevations. Increasing stream development for domestic, industrial, and agricultural demands raises concerns about the impact of diversions on stream resources (invertebrates, fish, riparian vegetation, water quality; Risser and Harris 1989). The potential effects are numerous and depend upon the degree of alteration to the natural pattern of flow (Poff et al. 1997, Richter et al. 1997). In extreme cases, 100 % of the flow can be diverted for 6 - 10 months of the year causing nearly complete dewatering of downstream sections.

Research has demonstrated that stream communities are tightly linked to flow variation and instream hydraulic conditions (e.g Statzner and Higler 1986; Poff et al. 1997). For example, reduced flows caused a reduction in the growth and abundance of riparian plants (Stromberg and Pattern 1990, Smith et al. 1991). As processors of organic matter and a primary food for fish (Cummins 1992; Cummins and Merritt 1996), aquatic macroinvertebrates, like riparian vegetation, are crucial to nutrient cycling and energy flow through lotic ecosystems. Flow alterations and dams that reduce discharge and affect temperature, hydraulics, substrate, periphyton, and invertebrates in large rivers (Ward and Stanford 1979; Petts 1984) might also alter benthic invertebrate communities in small streams.

Although the impact of dams on large river ecosystems has been the focus of numerous studies (e.g. Boon 1988; Hauer et al. 1989; Rader and Ward 1988; Stanford and Ward 1989), investigations on the affects of small diversions in high elevation headwater streams are few. We are not aware of a single

study in the United States. Research from outside the United States provides contradictory results that vary from no effect (Roy and Messier 1989; Castella et al. 1995) to reductions in invertebrate diversity and abundance (O'Keefe and De Moor 1988; Dudgeon 1992, Petts and Bickerton 1994, Englund and Malmqvist 1996).

The object of this study was to examine the influence of flow reduction and dewatering on macroinvertebrates in headwater streams of the Colorado Rocky Mountains. Specifically, we sampled invertebrates for one year upstream and downstream from diversions on three tributaries in the St. Louis watershed that varied from severe to mild flow alterations.

Site Descriptions

Sites were chosen upstream and downstream from diversions on three streams (St. Louis Creek, West St. Louis Creek and East St. Louis Creek) in the St. Louis Creek watershed 137 km west of Denver, Colorado on the western slope of the central Rocky Mountains, USA. Both East and West St. Louis Creeks are second order tributaries to St. Louis Creek which is the main channel (3rd order) draining the Fraser Experimental Forest. St. Louis Creek is a tributary of the Fraser River which flows to the Colorado River. The St. Louis Creek watershed (85.2 km^2) is typical of other watersheds in the region, where 95 percent of stream run-off is derived from snow melt with 5% from summer rainfall (Garstka et al. 1958). The annual hydrograph is dominated by a peak discharge which generally occurs in mid-June (Alexander et al. 1985). East and West St. Louis Creeks are primarily high gradient, narrow, confined, step-pool tributaries where the substrate is dominated by large, stable boulders (Ryan 1994). Riparian vegetation consists of lodgepole pine (Pinus contorta), Engelmann spruce (Picea engelmannii), and sub-alpine fir (Abies lasiocarpa). The mainstem (St. Louis Creek) is a riffle-pool stream with gravel and cobble

sized alluvial substrates (Ryan 1994). Riparian vegetation is similar to the east and west tributaries, except that unconfined sections are dominated by willows (Salix spp.).

Water collected from this watershed is used by the city of Denver, Colorado and comes from eight, out of a possible fourteen, second order tributaries, that have been dammed and in use since 1957 (Ryan 1994). A USGS gauging station located at the base of the watershed recorded the total annual yield of undiverted water which was 11.8 million m^3 during the course of this study, the 1993 - 1994 water year. The mean annual discharge for 22 years prior to and 34 years following diversion was 32 million m^3 and 18 million m^3, respectively (Ryan 1994). The average annual discharge following diversion (18 million m^3) corresponds to the lowest annual discharge prior to diversion. Unlike highly regulated dams on large rivers (e.g. Colorado River; Rader and Ward 1988), the amount of water allowed to pass downstream from the St. Louis Cr. and it's tributaries is not prescribed by agreements and law but can vary on a daily basis depending on the discretion and needs of the Denver Water Commission. The Denver Water Board is responsible for filling local storage reservoirs, while avoiding overfill which can weaken dam structures. Consequently, intra-annual flow variability downstream from diversions will fluctuate on short time scales and at irregular intervals, especially during runoff, depending on the starting level of the reservoir, snowpack height, and prevalence of spring and summer rain storms. There are no records or long-term flow data documenting when specific diversions are in operation.

Methods

From April to October was a season of rapid flow fluctuations as diversion gates were frequently opened and closed as management sought to fill, but not overfill, local reservoirs. Diversion gates were set and flow

fluctuations tended to stabilize in the fall and winter (November to March). Streams were classified a priori as to the degree of impact. St. Louis Creek was never dewatered and some aspect of all components of the natural flow regime, most baseflows and even channel-maintaining high flows, were transported downstream (low impact). During the season of infrequent flow fluctuations (November to March) only approximately 25 % of the baseflows were diverted. Most flow in the east and west tributaries was diverted for approximately 10 to 11 months annually (high impact). As in the mainstem, both tributaries were subject to seasons of frequent (April - October) and infrequent (November - March) flow fluctuations. During water abstraction, East St. Louis Creek was dewatered for 40 m downstream from the dam, whereas leakage from a faulty diversion structure prevented complete dewatering of West St. Louis Creek. In contrast to St. Louis Cr., therefore, 100 % (East St. Louis Cr.) to nearly 100 % (West St. Louis Cr.) of the flow was diverted during the season of infrequent flow fluctuations (November - March). Because of groundwater inputs, flow recovered to 0.002 $m^3 s^{-1}$ at 400 m downstream in East St. Louis Creek.

Two invertebrate samples were collected from three riffles upstream and downstream from each diversion (6 samples at 6 sites) once a month from October 1993 to October 1994 using a standard Surber sampler (250 µm mesh). The first 3 riffles encountered were sampled at all upstream locations, whereas riffles varied from 30 - 50 m downstream on West St. Louis Creek and the mainstem to 400m downstream on East St. Louis Creek. Invertebrates were not collected from the intermittent section immediately downstream from the dam on East St. Louis Cr. We chose a site 400 m downstream in a permanent stream section because we were more interested in the effects of reduced flows rather than the impact of flow intermittency. Invertebrate samples were preserved in 4% Formalin and identified to the lowest possible taxonomic level except for

Chironomidae, Oligochaeta, and Ostracoda. Also, invertebrates were not collected from East St. Louis Cr. from December through March because the site was not accessible due to harsh weather conditions.

Most flow measurements at each site were either volumetrically determined or calculated using the cross-sectional method (Gordon et al. 1992). Flow upstream on East St. Louis Cr. was provided by a permanent Forest Service gauging station. Temperature was continuously recorded upstream and downstream at each site using StowAway® (Onset Computer Corp.) data loggers. Oxygen, pH, and conductivity were also measured in the field every other month at each site.

Statistical Analysis

Invertebrate analyses were restricted to separate upstream versus downstream comparisons for all three streams. Because of differences in geomorphology, size, and flow there were no between stream comparisons. Average invertebrate community metrics (total invertebrate density and species richness) were divided into two seasons, frequent (April through October), and infrequent (steady diversion) flow fluctuations (November through March). Upstream versus downstream comparisons were analyzed separately for each season. A paired t-test (upstream versus downstream) was used to determine differences in average invertebrate density and richness within the same flow diversion season for each stream. These data often required a log transformation to meet parametric assumptions of normality and equal variances as determined by Shapiro-Wilk's and Bartlett's tests, respectively. Even if there were no upstream versus downstream differences in mean density and richness, we suspected that downstream invertebrate metrics might fluctuate (time and space) more than upstream density and richness. Therefore, the coefficient of variation (e.g. Palmer et al. 1997) based

on total invertebrate density per sample was also compared (upstream versus downstream) using a Kruskal-Wallis non-parametric test.

Results

Physical and Chemical Comparisons

Mean annual discharge was either reduced (mainstem St. Louis Cr.) or vastly reduced (West and East St. Louis Creeks) downstream from diversions (Table 1). Even though East St. Louis Cr. is completely dewatered when diverted, downstream flow estimates were higher than West St. Louis Cr. because the study site was 400 m downstream on East compared to 30 - 40 m downstream on West St. Louis Cr. Although oxygen and pH were similar between upstream and downstream sites, there were important differences in temperature and conductivity. Higher conductivity at downstream sites on West and especially East St. Louis Creeks reflected greater proportions of groundwater to surface water (Table 1). In East St. Louis, the entire flow downstream from the dam was attributed to groundwater during water abstraction. West St. Louis also showed high groundwater inputs, but not as high as in East St. Louis Cr. because of surface water leakage from the dam. Water was never completely diverted on the mainstem so, conductivity was similar between upstream and downstream sites. The dam on the mainstem was built in an open clearing, so it's small (< 0.5 ha), shallow (< 2.5 m) reservoir was not shaded from the afternoon sun. Consequently, maximum water temperature and the number of annual degree days increased by 2 and 70 C, respectively, from just a few meters upstream to a few meters downstream from the dam. The number of annual degree days were also 124.6 and 127.3 C greater downstream from West and East St. Louis Cr., respectively. Both East and West St. Louis Creeks and their dams were heavily shaded by riparian vegetation. Therefore, these temperature increases were attributed to

groundwater inputs during the winter at downstream sites and not insolation as in the mainstem.

Invertebrate Comparisons

Downstream mean invertebrate density during the season of infrequent flow fluctuations (nearly 100% of baseflows were diverted) was 50% reduced in West St. Louis Creek. Except for Diptera, the downstream density of all invertebrate groups was reduced, especially Ephemeroptera which were 91% lower (Table 2). The downstream density of mayflies would have been even further reduced if not for Ameletus spp. which increased by 41% downstream during the period of constant diversion and infrequent flow fluctuations (Table 3). Similarly, downstream invertebrate density would have been much lower if not for a slight increase in chironomids, the most abundant taxa at both upstream and downstream sites. Chironomids and ostracods comprised 75% of the downstream assemblage, whereas chironomids, mayflies (especially B. bicaudatus), and ostracods comprised 76% of the upstream assemblage (Tables 2 and 3). Baetis bicaudatus, the most abundant upstream species, was reduced from 4288 m^{-2} to 63 m^{-2} in the downsteam section (Table 3). In contrast, mean invertebrate density was 57% greater downstream than upstream in St. Louis Creek also during the season of infrequent flow fluctuations when most baseflows (approximately 75%) were transported downstream (Table 2). In fact, the density of all invertebrate groups, especially Ephemeroptera (75% increase) and Plecoptera (68% increase), was greater downstream in the mainstem during this time period (Table 2). Much of the downstream increase in mayfly density was attributed to Baetis bicaudatus which was 68% higher than upstream (Table 3). During the season of frequent flow fluctuations, there were no significant differences (upstream versus downstream) in the density of invertebrates in any of the three streams (Table 2). In fact, upstream versus downstream

densities of most invertebrate taxa was very similar during this time period (Table 3). Some notable exceptions were higher downstream densities of Diptera and Coleoptera in West St. Louis Cr. and non-Insecta, (especially Ostracoda) and Ameletus spp. in East St. Louis Creek (Table 3).

Except for West St. Louis Cr. during infrequent flow fluctuations, taxa richness was nearly equal upstream and downstream from each diversion during both diversion seasons. The average upstream versus downstream richness per sample in the mainstem (20.3 vs. 20.9), East (17.4 vs. 16.0) and West (21.6 vs. 15.3) tributaries was not significantly ($P > 0.3$) different. However, average downstream richness (15.0) per sample in West St. Louis Cr. during the season of infrequent flow fluctuations was 27% lower ($P = 0.01$) than upstream (25.6). This same pattern is reflected in the total number of taxa collected at each site as the only large upstream (45) versus downstream (38) difference was in West St. Louis Cr. during the season of constant diversion (Table 2). Ten taxa, including five relatively abundant species (Neothremma alicia, Hesperoperla pacifica, Megarcys signata, Taenionema pallidum, and Polycelis coronata), were absent from the downstream section, whereas only 2 rare species (Paraleptophlebia sp. and Amphinemura banksi) were apparently absent upstream but present in the downstream section. Of the 10 taxa absent downstream in West St. Louis Cr. during infrequent flow fluctuations, all but 2 (Bibiocephala grandis and Polycelis coronata) recovered or were present downstream during the period of frequent flow fluctuations (April - October).

The only significant difference (upstream versus downstream) in the average coefficient of variation based on total invertebrate density and richness was in West St. Louis Creek (Table 4). Downstream variation in density and richness during the period of frequent flow fluctuations was 33% and 63% greater than upstream, respectively. A similar, but statistically insignificant

trend (P values were slightly greater than 0.05) of greater variation in density and richness also occurred in East St. Louis Creek (Table 4).

Discussion

In the mainstem (St. Louis Cr.), downstream invertebrate abundance and diversity was not reduced during either periods of frequent or infrequent flow fluctuations. There was no indication that mild diversion (all components of the natural flow regime were transported downstream) had a harmful impact on the invertebrate assemblage. In fact, during the period (November - March) of constant diversion (approximate 25 % reduction in baseflows) and infrequent flow fluctuations, invertebrate downstream densities were 57% higher than upstream. There are at least 3 potential explanations for greater downstream densities of invertebrates during the fall and winter on the mainstem. First, several authors have suggested that flow abstraction can cause a reduction in the wetted perimeter of downstream sections resulting in a concentration of invertebrates and the absence of upstream versus downstream differences (Roy and Messier 1989, Castella et al. 1995, Englund and Malmqvist 1996). However, fall and winter flow reductions in St. Louis Cr. did not cause a reduction in the wetted perimeter. Higher densities were not caused by invertebrates concentrating in a smaller area as the wetted perimeter diminished. Second, a reduction in spring scouring flows might also result in higher downstream densities. Much of the reduction in high flows occurred during the ascending and descending limbs, since most peak flows were passed downstream. If reduced scouring flows had a positive impact on invertebrate density, then we might expect higher downstream abundances following runoff. However, mean invertebrate densities (upstream versus downstream) were very similar (3761.9 m^{-2} versus 3295.6 m^{-2}) in the summer following snowmelt runoff. Third, warmer downstream temperatures may result in a

more favorable habitat for invertebrate growth and development. The St. Louis watershed is one of the coldest on record (Alexander et al. 1985). Outside of Alaska, Fraser, Colorado (10 km from our study sites) is consistently the coldest location in the United States. Temperature may be one of the primary factors limiting the growth and development of invertebrates in this watershed. If so, then the increased number of annual degree days (70) may result in larger more fecund females and higher downstream recruitment of invertebrates during the summer and fall. The thermal equilibrium hypothesis (Vannote and Sweeney 1980) predicts that aquatic insect body size and fecundity and, consequently, population density will be maximized along elevational gradients where the thermal regime is optimal for growth and development. Temperature, especially at the edge of a species elevational distribution (e.g. Rader and Ward 1990), may be one of the most important limiting factors in determining population abundance. Previous research in a neighboring watershed indicated that many of the taxa in this study were at or near the upper limit to their elevational distribution (Ward 1980, Ward 1986). Higher temperatures may also cause an increase in algal and detrital (faster decomposition rates) food resources. Therefore, in addition to increased growth and recruitment, downstream densities may also increase as upstream taxa drift into and remain in the downstream section with warmer temperatures and higher resource availability. We suggest that higher temperatures is a plausible explanation for greater downstream invertebrate densities during the fall and winter in St. Louis Creek.

In contrast to the mainstem, negative effects of vastly reduced flows in the severely diverted West St. Louis Creek appear to outweigh the potentially positive influence of warmer downstream temperatures. Despite an annual increase of 124.6 degrees, invertebrate density and species richness were 50%

and 16% reduced, respectively, in the downstream section during the fall-winter period of constant diversion and infrequent flow fluctuations. If not for taxa with the apparent ability to exploit low flow conditions (chironomids, ostracods, and Ameletus spp.) downstream invertebrate densities would have been vastly reduced. Other studies also found that Chironomidae were common or increased under low-flow conditions (Wright and Berrie 1987, Boulton and Lake 1992). We believe that the greater downstream densities of these taxa indicated a real tolerance to and ability to exploit low flow conditions and was not a result of compaction due to a reduction in the wetted perimeter. An increase in density because of a reduction in the wetted perimeter is a temporary phenomena. Lotic invertebrate communities appear capable of rapid adjustments to reduced flows (e.g. Minshall and Winger 1968, Poff and Ward 1991, Boulton and Lake 1992). As flows decline and invertebrates concentrate in a smaller area, the community can rapidly adjust (e.g. drift) to both density independent (e.g. stranding, respiratory stress), and density dependent factors (competition and predation). Therefore, consistently high densities associated with prolonged periods of constant reduced flows, as in this study, is indicative of a real tolerance to low flow conditions.

Most of the mayflies (Baetis bicaudatus, Drunella coloradensis, D. doddsi, Epeorus deceptivus, Rhithrogena robusta), plus Doddsia occidentalis, Neothremma alicia, and Simuliidae had the greatest downstream reductions in density and appeared the least tolerant of low flow conditions. Since mayflies are an important food resource for salmonids in the Rocky Mountains, diversions may have harmful indirect effects on fish food resources. Plus, the downstream absence of a few rarer taxa (Hesperoperla pacifica, Megarcys signata, and Polycelis coronata) is worth noting because of their potential importance as predators. It is also important to emphasize that except for a few

species with low drift propensities (P. coronata, D. occidentalis, and Bibiocephala grandis; Rader 1997), all taxa diminished or absent downstream in W. St. Louis Cr. during the fall and winter recovered during the spring-summer period of frequent flow fluctuations. In fact, there was no upstream versus downstream differences in mean invertebrate density or diversity during the spring and summer period of frequent flow fluctuations in any of the three streams. Recolonization by opening the gates and re-establishing free-flowing conditions has been frequently cited as one of the primary reasons for the absence of downstream effects due to water diversion (Delucchi 1988; DeBrey and Lockwood 1990; Dudgeon 1992; Englund and Malmqvist 1996). However, these studies have examined invertebrate responses using central tendency measures (e.g. mean density) without considering variance. Palmer et al. (1997) emphasized the importance of examining both the mean and variance in order to identify and understand the response of invertebrates to altered environmental conditions. The coefficient of variation based on both total invertebrate density and richness per sample was significantly greater downstream on West St. Louis and nearly significantly greater in the eastern tributary during the period of frequent flow fluctuations. Although means were not different, the variance was greater downstream. This result indicates that the spatial distribution and temporal occurrence of invertebrate populations within these downstream communities varied far more than their upstream counterparts. Depending on the frequency with which free-flowing conditions are re-established, many invertebrate populations (especially mayflies and some stoneflies) will diminish and even go temporarily extinct (e.g. Hesperoperla pacifica, Megarcys signata, Neothremma alicia, Polycelis coronata). Therefore, downstream communities in the heavily diverted West and East St. Louis tributaries appear to fluctuate between two stable endpoints; a

low-flow community dominated by chironomids and ostracods and a natural-flow community dominated by mayflies, chironomids, stoneflies, and ostracods. (If biomass had been measured, the importance of ostracods and stoneflies would have decreased and increased, respectively).

Conclusions

Our results suggest that diversions can have variable effects on benthic communities in headwater streams of the Rocky Mountains depending on the degree of alteration to the natural flow regime. Invertebrates appeared resilient to mild diversion where some aspect of all components of the natural flow regime were transported downstream. However, invertebrate abundance and diversity declined and spatial and temporal variation increased in our more heavily diverted headwater streams (West and East St. Louis tributaries). In these small Rocky Mountain streams, Ephemeroptera appear to be the best indicators of the effects of diversion. Humans have reduced the capacity of river ecosystems to sustain natural diversity and production by severing or compromising the dynamic interactive pathways of the river continuum (Zwick 1992, Stanford et al. 1996). Altered flow regimes may be the most risky and pervasive influence of humans on river landscapes world-wide (Dynesius and Nilsson 1994). With concerns for the conservation of biodiversity and the sustainability of ecosystems, the demands on water resources must be considered in relation to ecological needs (Petts 1996; Poff et al. 1997) Future research could use mayflies as indicator organisms to focus on the quantity and timing of water abstraction. How much water and when can it be diverted to minimize risks to downstream ecological resources?

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Table 1. Average physical and chemical characteristics upstream and downstream from each diversion. Discharge was the average based on periodic readings during diversion/water abstraction except upstream on East St. Louis Cr. which was the annual average of continuous readings from a Forest Service gauging station.

	St. Louis		West St. Louis		East St. Louis	
	Upstream	Downstream	Upstream	Downstream	Upstream	Downstream
Slope (m/m)	0.018	0.014	0.020	0.025	0.074	0.047
Elevation (m)	3006	2996	2926	2914	3032	2955
Discharge ($m^3 s^{-1}$)	0.638	0.402	0.134	0.001	0.182	0.002
Mean Annual Temperature (°C)	5.5	5.7	5.3	6.1	5.0	6.0
Temperature Max./Min. (°C)	11.9/0.0	13.9/-0.2	11.1/0.0	11.1/0.0	9.4/-0.2	9.5/0.2
Annual Degree Days (°C)	863.7	933.6	830.9	955.5	811.6	938.8
Oxygen ($mg\ l^{-1}$)	9.9	10.6	11	9.7	11.2	10.6
pH	6.8	6.6	6.7	6.7	6.7	6.5
Conductivity (µS)	102.4	83.1	105.0	611.2	74.6	823.6

Table 2. Average density (#·m^{-2}) and relative abundance (%) of invertebrate orders plus, the mean seasonal density and total seasonal richness upstream and downstream from diversions during frequent (April - October) and infrequent (November - March) flow fluctutations. Standard errors are in parentheses and "*" = $P \leq 0.05$.

		St. Louis Cr.				West St. Louis Cr.				East St. Louis Cr.			
		Upstream		Downstream		Upstream		Downstream		Upstream		Downstream	
Season	Taxa	Density	%	Density	%	Density	%	Density	%	Density	%	Density	%
Frequent	Diptera	773.3 (325.6)	20.5	891.8 (226.0)	27.0	1669.3 (277.5)	31.4	2747.6 (1135.3)	46.8	1413.7 (417.4)	28.5	1675.0 (748.6)	30.3
	Ephemeroptera	1608.8 (382.0)	42.7	1316.2 (262.0)	39.9	1639.5 (414.2)	30.9	1002.5 (477.2)	17.1	1577.9 (395.0)	31.8	1431.1 (532.2	25.9
	Trichoptera	114.8 (33.7)	3.1	116.2 (31.0)	3.5	112.2 (17.4)	2.1	184.1 (95.0)	3.1	329.5 (68.7)	6.6	238.3 (58.1)	4.3
	Plecoptera	741.3 (146.0)	19.7	697.7 (91.5)	21.2	957.3 (140.9)	18.0	920.5 (299.5)	15.7	802.1 (162.9)	16.2	835.1 (206.0)	15.1
	Coleoptera	7.9 (3.8)	0.2	15.0 (5.4)	0.5	31.4 (20.3)	0.6	106.2 (44.0)	1.8	0.3 (0.3)	0.1	0.3 (0.3)	<0.1
	Non-Insecta	518.1 (151.4)	13.8	258.8 (97.4)	7.9	900.8 (191.6)	17.0	912.6 (518.3)	15.5	834.7 (283.6)	16.8	1356.0 (657.7)	24.4
	Mean Seasonal Density	3761.9 (833.1)	-	3295.6 (535.3)	-	5310.5 (609.5)	-	5873.5 (2437.0)	-	4958.1 (1100.7)	-	5534.9 (1998.1)	-
	Total Richness	49		50		49		51		51		52	
Infrequent													
	Diptera	2427.9 (916.2)	36.8	3609.4 (505.4)	34.8	3806.4 (968.6)	27.0	4006.7 (1913.1)	56.7	-	-	-	-
	Ephemeroptera	2166.9 (499.4)	32.8	3797.1 (257.5)	36.5	5564.4 (1340.5)	39.5	507.2 (200.1)	7.2	-	-	-	-
	Trichoptera	199.7 (72.0)	3.0	217.0 (15.3)	2.1	182.9 (56.6)	1.3	130.7 (62.6)	1.9	-	-	-	-
	Plecoptera	1111.9 (84.1)	16.9	1872.8 (149.5)	18.0	1394.9 (257.1)	9.9	849.6 (173.6)	12.0	-	-	-	-
	Coleoptera	13.8 (3.9)	0.2	37.7 (3.1)	0.4	81.9 (22.5)	0.6	69.3 (19.4)	1.0	-	-	-	-
	Non-Insecta	680.3 (107.7)	10.3	850.6 (72.7)	8.2	3048.1 (661.0)	21.7	1495.0 (355.3)	21.2	-	-	-	-
	Mean Seasonal Density	6600.4 (1393.9)	-	10384.0* (205.0)	-	14078.6 (1739.5)	-	7058.4* (2357.5)	-	-	-	-	-
	Total Richness	45	-	47	-	45	-	38	-	-	-	-	-

Table 3. Average density (# m^{-2}) of invertebrates upstream (Up) and downstream (Down) from diversions during frequent (April - October) and infrequent (November - March) flow fluctuations.

Taxa	St. Louis Cr.				West St. Louis Cr.				East St. Louis Cr.	
	Infrequent		Frequent		Infrequent		Frequent		Frequent	
	Up	Down	Up	Down	Up	Down	Up	Down	Up	Down
DIPTERA	-	-	-	-	-	-	-	-	-	-
Blephariceridae	-	-	-	-	-	-	-	-	-	-
Agathon sp.	-	-	1.8	0.2	-	-	-	-	-	-
Bibiocephala grandis	1.8	2.7	5.16	3.1	0.6	-	-	-	0.8	-
Philorus sp.	-	-	-	0.9	-	-	-	-	-	-
Chironomidae	2365.4	3479.4	701.1	799.8	3523.3	3925.2	1549.3	2571.2	1348.3	1592.5
Ceratopogonidae										
Palpomyia sp.	17.3	55.3	34.6	50.9	2.1	2.9	5.8	15.6	-	0.3
Empididae										
early instars	-	-	-	-	-	-	-	0.6	0.8	-
Chelifera sp.	-	11.7	-	0.5	31.0	32.8	11.1	37.4	4.1	40.4
Clinocera sp.	4.2	2.4	2.9	0.3	-	-	1.5	0.3	8.2	4.2
Oreogeton sp.	-	1.8	0.9	0.2	1.2	5.0	0.5	0.3	0.8	1.7
Dixidae										
early instars	-	-	0.9	-	3.6	-	-	-	-	1.2
Dixa sp.	-	-	-	-	5.9	-	0.3	1.2	-	-
Tipulidae										
Dicranota spp.	9.3	14.1	3.4	5.6	40.4	17.4	16.1	16.6	17.2	12.6
Hexatoma sp.	1.2	1.2	2.5	2.9	5.9	6.3	2.3	4.4	-	-
Limnophila sp.	-	0.9	-	-	-	-	0.5	-	-	-
Limonia sp.	-	-	0.9	-	-	-	-	-	-	-
Molophilus sp.	-	-	-	-	-	-	-	-	-	1.2
Pedicia sp.	-	4.8	-	-	-	-	-	0.6	0.3	-
Tipula spp.	-	-	-	-	-	-	-	-	0.3	-

Table 3 (continued)

Taxa	St. Louis Cr.				West St. Louis Cr.				East St. Louis Cr.	
	Infrequent		Frequent		Infrequent		Frequent		Frequent	
	Up	Down	Up	Down	Up	Down	Up	Down	Up	Down
Simuliidae										
Prosimulium spp.	27.5	35.3	18.3	19.8	81.3	4.5	44.4	95.4	32.8	20.9
Simulium spp.	1.2	-	0.9	6.6	109.9	12.6	37.4	4.1	-	-
Thaumaleidae										
early instars	-	-	-	-	-	-	-	-	0.3	-
EPHEMEROPTERA										
Baetidae										
Baetis bicaudatus	996.5	3058.2	735.3	786.4	4288.1	62.9	1104.9	490.9	627.7	436.4
Baetis tricaudatus	-	-	21.7	30.7	-	-	18.7	-	5.4	0.5
Ephemerellidae										
Drunella early instars	178.7	108.2	40.4	18.7	154.2	17.1	19.7	7.5	34.3	21.0
Drunella coloradensis	49.3	21.5	8.9	13.9	50.2	0.9	6.1	8.9	31.8	27.5
Drunella doddsi	88.8	118.1	22.5	15.1	-	-	6.7	0.3	0.5	0.3
Heptageniidae										
early instars	230.4	223.6	51.3	11.1	254.1	41.9	7.1	22.0	25.6	30.2
Cinygmula spp.	257.9	8.9	212.2	109.1	502.1	100.9	218.8	303.0	255.4	440.7
Epeorus deceptivus	105.8	13.1	180.9	83.9	71.1	7.5	56.9	50.3	329.9	222.9
Rhithrogena robusta	228.1	221.8	319.3	232.5	58.6	6.9	157.7	29.3	219.6	146.9
Leptophlebiidae										
Paraleptophlebia spp.	-	2.4	-	-	-	6.8	-	15.2	-	-
Siphlonuridae										
Ameletus spp.	31.4	21.2	16.1	13.8	185.9	262.3	42.9	74.9	47.7	103.7
Tricorythidae										
Tricorythodes minutes	-	-	-	0.9	-	-	-	-	-	-
TRICHOPTERA										
Glossosomatidae										
early instars	-	-	0.9	-	-	-	-	-	-	-

Table 3 (continued)

Taxa	St. Louis Cr.				West St. Louis Cr.				East St. Louis Cr.	
	Infrequent		Frequent		Infrequent		Frequent		Frequent	
	Up	Down	Up	Down	Up	Down	Up	Down	Up	Down
Anagapetus debilis	22.7	11.4	25.8	22.3	-	-	1.0	14.5	5.6	9.9
Glossosoma spp.	43.9	55.3	24.9	38.2	2.9	-	-	28.4	1.3	14.5
Limnephilidae										
early instars	3.6	-	0.2	-	7.2	2.7	1.3	2.2	-	7.7
Allomyia gnathos	-	-	-	-	-	-	-	-	1.5	-
Chyranda centralis	0.6	4.8	0.2	-	3.6	15.3	-	1.0	5.6	11.1
Ecclisomyia maculosa	20.9	11.4	1.8	3.8	9.6	79.9	0.5	13.4	96.6	69.9
Hesperophylax sp.	-	-	-	0.3	-	-	-	-	-	0.5
Psychoronia costalis	-	-	-	-	-	-	-	-	1.0	0.3
Rhyacophilidae										
Rhyacophila spp.	10.2	14.4	8.1	4.9	2.4	9.8	4.2	51.8	20.2	15.4
Rhyacophila alberta	26.9	17.0	13.9	9.6	39.2	19.1	25.7	31.1	110.2	83.5
Rhyacophila angelita	-	-	-	-	-	-	-	-	0.3	2.2
Rhyacophila brunnea	13.8	23.3	5.0	9.1	3.3	1.4	5.4	15.4	-	3.8
Rhyacophila hyalinata	12.9	13.2	10.9	7.2	7.8	-	6.2	0.3	31.3	4.4
Rhyacophila pellisa	3.6	26.0	4.6	9.8	21.8	2.4	20.9	1.0	0.8	0.5
Rhyacophila verrula	-	-	-	-	-	-	-	19.8	1.3	1.3
Uenoidae										
Neothremma alicia	0.6	21.2	-	-	85.2	-	47.1	5.2	10.3	3.8
Oligophlebodes sp.	40.1	19.1	16.2	10.8	-	-	-	-	43.6	9.5
PLECOPTERA										
early instars	5.4	-	-	1.1	16.7	5.7	4.4	9.8	4.9	-
Euholognatha nymph	-	-	-	1.1	-	-	-	-	-	-
Systellognatha nymph	-	-	0.3	1.8	-	-	1.2	-	-	-
Capniidae										
early instars	-	-	5.4	5.4	14.4	10.2	37.2	29.2	14.1	2.3

Table 3 (continued)

Taxa	St. Louis Cr.				West St. Louis Cr.				East St. Louis Cr.	
	Infrequent		Frequent		Infrequent		Frequent		Frequent	
	Up	Down	Up	Down	Up	Down	Up	Down	Up	Down
Capnia spp.	36.5	7.8	5.9	10.3	30.5	32.4	42.0	65.2	38.7	33.5
Eucapnopsis brevicauda	0.6	-	0.7	1.4	8.4	-	9.2	0.9	23.3	5.1
Chloroperlidae										
early instars	37.1	49.6	14.8	18.7	52.6	102.4	14.9	61.0	5.4	13.1
Plumiperla diversa	11.4	-	15.1	12.8	26.3	1.9	9.7	16.9	0.5	8.8
Suwallia spp.	42.1	-	22.4	0.7	4.5	16.1	1.0	6.8	-	-
Sweltsa spp.	67.3	60.9	100.4	101.6	123.7	175.8	133.5	179.3	114.5	197.3
Leuctridae										
Paraleuctra spp.	60.1	91.5	60.6	76.4	145.3	60.1	167.8	96.3	45.1	63.0
Nemouridae										
early instars	-	-	-	0.9	-	-	-	1.3	-	2.3
Amphinemura banksi	0.6	2.4	0.5	-	-	1.4	0.3	0.3	1.0	10.7
Podmosta sp.	-	-	-	8.1	-	-	0.3	44.2	1.0	4.1
Zapada spp.	516.5	815.4	60.8	83.6	625.9	356.7	107.9	131.3	125.0	104.4
Zapada cinctipes	4.5	1.8	1.4	4.4	31.1	12.6	146.3	138.1	45.6	86.2
Zapada haysi/oregonensis	157.5	248.9	179.8	149.4	46.6	54.7	113.2	61.6	248.5	229.9
Perlidae										
Hesperoperla pacifica	-	-	-	-	24.2	-	44.5	1.1	-	1.0
Perlodidae										
early instars	10.8	9.6	16.1	6.9	17.0	-	12.3	22.2	10.5	25.4
Isoperla spp.	5.1	23.9	3.3	4.5	6.3	8.2	3.8	2.4	3.3	3.4
Isoperla phalerata	-	1.2	-	-	-	7.6	-	11.7	-	0.8
Kogotus modesta	-	-	0.2	-	-	-	0.3	-	-	-
Megarcys signata	4.8	11.7	8.1	9.5	10.8	-	7.5	5.3	11.3	5.4
Taeniopterygidae										
early instars	3.6	7.2	2.2	4.0	13.2	-	4.9	27.0	2.6	1.2
Doddsia occidentalis	145.6	462.1	202.3	166.8	180.8	3.8	58.3	7.1	83.0	25.2
Taeniopteryx pallidum	2.7	78.9	41.0	28.4	16.7	-	36.6	1.5	23.8	11.3

Table 3 (continued)

Taxa	St. Louis Cr.				West St. Louis Cr.				East St. Louis Cr.	
	Infrequent		Frequent		Infrequent		Frequent		Frequent	
	Up	Down	Up	Down	Up	Down	Up	Down	Up	Down
COLEOPTERA										
Heterlimnius corpulentus	13.8	37.7	7.9	15.0	81.9	69.3	31.4	106.2	0.3	0.3
COLLEMBOLA	-	4.8	2.8	0.8	3.6	2.4	13.6	7.2	15.4	10.9
HYDRACARINA	17.9	8.4	7.4	8.3	53.5	14.9	55.3	177.6	39.2	24.7
NEMATODA	20.6	51.7	6.2	13.1	31.1	10.8	5.7	9.6	7.2	6.5
ANNELIDA										
OLIGOCHAETA	318.0	501.2	357.9	132.4	374.2	197.6	318.6	162.6	396.6	519.7
OSTRACODA	286.9	279.8	105.6	91.5	2580.6	1269.4	494.1	556.6	301.8	745.1
TURBELLARIA										
Polycelis coronata	36.8	4.8	38.5	12.9	5.1	-	13.4	-	74.6	50.7